CHAPTER 7

THE DESIGN, FUNCTION AND CALIBRATION OF LARGE INDIRECT OPEN-CIRCUIT RESPIRATION CHAMBERS FOR ENERGY METABOLISM STUDIES ON GROUPS OF POULTRY AND A PRELIMINARY STUDY ON BROILER BREEDERS

Chapter 7

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7.1 INTRODUCTION

The differences in biological response between layer-type and broiler breeder birds to feed restriction were highlighted previously (see Chapter 1, Section 1.4). Studies so far presented in this thesis have investigated various aspects of the production (Chapter 3), energy metabolism (Chapter 6) and body composition (Chapter 5) of layer-type birds both during and subsequent to common feed restriction programmes. Commercial management practices used for the rearing of broiler breeders, and during egg production, differ substantially from those used for layer-type birds. During the rearing period, broiler breeders are usually subjected to a greater severity of feed restriction relative to *ad libitum* feed consumption, compared with layer-type birds, because of the markedly greater feed intake by these birds in relation to their requirements. Further feed restriction is usually implemented during egg production, often according to stage of production. The effects of these practices on the energy metabolism of broiler breeders are unknown, but there is good evidence to suggest that some alteration may occur (MacLeod and Shannon 1978; MacLeod *et al.* 1979).

Therefore, investigations on the energy metabolism and production responses of broiler breeder birds to feed restriction programmes were warranted not only on the important basis of the increased predicted magnitude of response in terms of egg production, but also for comparison with information already obtained on layer-type birds. Moreover, there is little available information on the energy metabolism and requirements of current broiler breeder strains. Female birds commercially available are derived from base flocks which have been intensively selected for liveweight gain and good egg production. Balnave *et al.* (1978) investigated the energetics of broiler breeders, but the results reported do not appear to be compatible with other studies on heavy breeds of birds (e.g. Waring and Brown 1965; Grossu *et al.* 1976). This may possibly indicate that the energy metabolism of Australian broiler breeders is different from that

predicted. Although information on the energy requirements of broiler breeders is usually derived either empirically or from data on layer-type birds, the mixture of different strains and breeds in broiler stock (Farrell 1975; MacLeod and Shannon 1978), varied selection criteria (Pym and Dillon 1977) and behavioural differences could result in an energy metabolism which is different from that of layer-type birds. Considerations such as these may be important in explaining the large responses reported for Australian broiler breeders due to rearing feed restriction (Pym and Dillon 1974; Watson 1976).

Calorimetric studies are labour intensive and present several theoretical and technical difficulties and it is important that such studies should strike a balance between theoretical considerations and the practical applicability of the results obtained. Energy metabolism studies conducted on poultry frequently used small numbers of birds (see Table 6.9, Chapter 6), and showed little regard for behavioural traits and adjustment to conditions which are prerequisites for normal production. Extrapolation of the results obtained from such studies to the practical situation, often the ultimate aim, may be of doubtful application. In addition, the time and labour required for calorimetric measurements have long been regarded as major limitations to energy metabolism studies, although some recently constructed poultry calorimeters were designed to overcome these problems (Misson 1974; Lundy *et al.* 1978). There is clear evidence available for a range of animal species to show that special cognisance must be taken of the effect of calorimetric measurements *per se* on energy metabolism (Blaxter 1974; Misson 1974).

Calorimetric studies commonly use classical methods (Brody 1945; Kleiber 1961; Blaxter 1962) to achieve variations in energy intake and retention which allow subsequent estimation of the efficiency of energy utilization and maintenance requirements. Starvation measurements are usually included (see Table 6.9, Chapter 6). Where these methods are regularly repeated the metabolic effects *per se* may be important. Also, if the aim of the energy metabolism studies is to explain observed production differences, as in the case of the investigation of restricted feeding, then the effects of such studies on production must be minimized. Certainly there would be large effects on the normal egg production patterns of birds due to regular periods of inadequate feed intake and starvation. This necessitated a reappraisal of the classical methods used for energy metabolism studies, and it was therefore planned that calorimetric measurements would be carried out on groups of birds on experimental

treatments without recourse to modification *pro rata* for estimation of energy metabolism. New large, open-circuit respiration chambers, which operate on indirect principles, were therefore constructed to house groups of poultry for the duration of an experiment. Problems such as individual variability in energy metabolism and behavioural changes due to experimental conditions were regarded as being minimized, and efficiency of equipment usage optimized, by the use of such chambers.

This chapter describes the design of the respiration chambers, their operation and calibration, and a preliminary experiment on broiler breeder hens which aimed to elucidate the special problems which may occur with these birds, and also to standardize data collection and calculation procedures. A secondary aim of the study was to provide initial information on the energy metabolism of broiler breeders.

7.2 MATERIALS AND METHODS

7.2.1 Design, function and operation of the respiration chambers

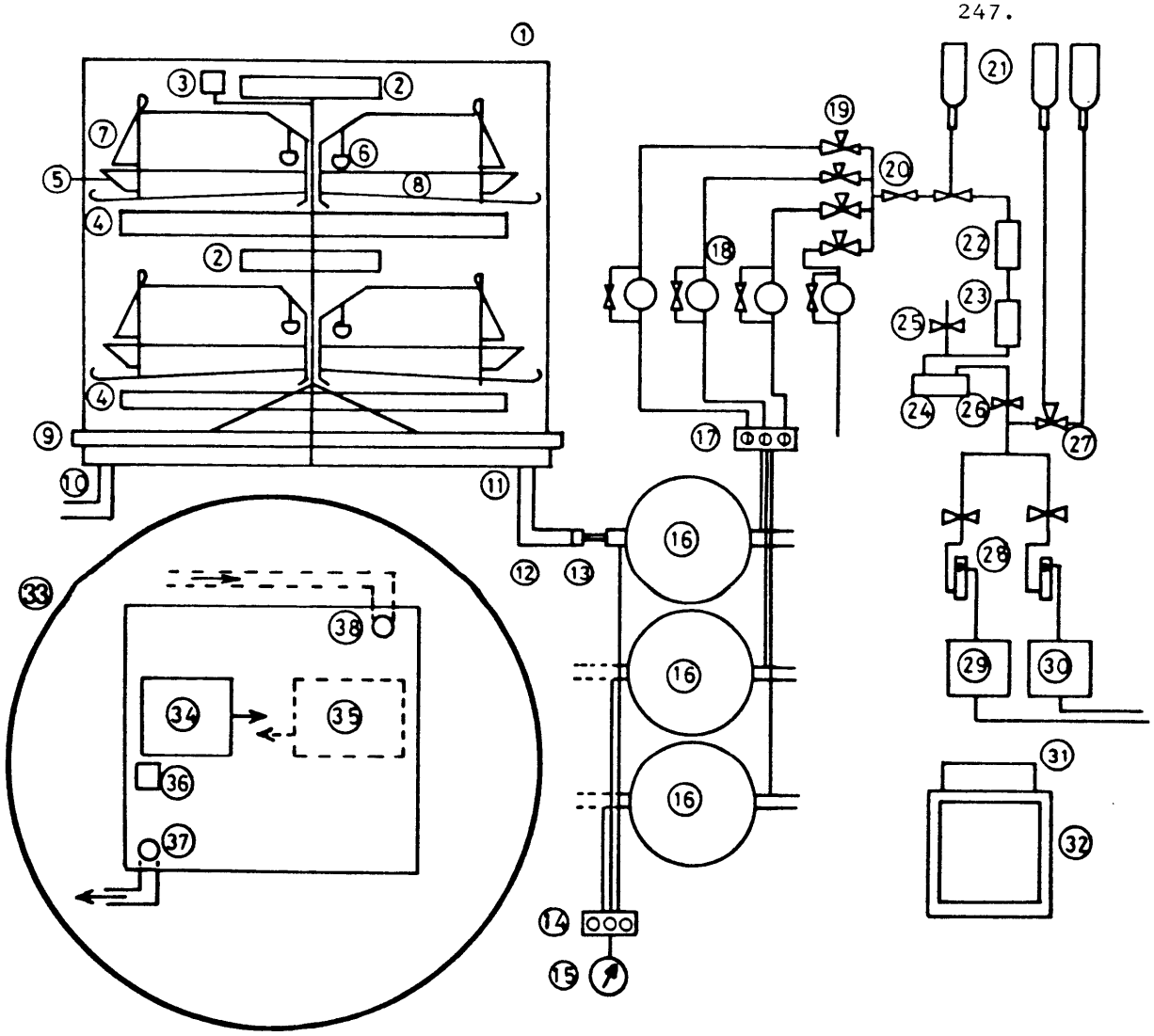
7.2.1.1 Design

The unit consists of three independent, open-circuit, indirect respiration chambers, a ventilation system, a flow and gas analysis system and a recorder. The main features of the chambers, which are maintained in an air-conditioned (20°C), light-proof room are given in Figure 7.1. Various aspects of the calorimeter system are shown in Plates 7.1, 7.2, 7.3 and 7.4. Lighting in the room is fluorescent and can be controlled by an automated timeclock (Venner Ltd., England).

7.2.1.2 Respiration chambers

Each chamber can hold either 24 immature pullets or adult layer-type birds, or 16 adult broiler breeder birds. Chambers (1.6 m length x 1.3 m width x 1.6 m height) were constructed with a basic framework of PVC conduit (20 mm diameter) which is covered with polyethylene plastic sheeting (0.4 mm gauge, Halifax Trading, Sydney, Australia). The plastic sheet was joined and sealed by heating. The galvanised sheet metal base, mounted on an iron framework 80 mm in height, has a water-filled channel (60 mm width x 90 mm height) around the perimeter. The plastic covered framework is lowered into this channel to provide an hermetic seal during periods of measurement of gaseous exchange.

There is a single cage unit positioned on the base of each chamber. Each cage unit (1.2 m length x 1.3 m width x 1.3 m height) consists of



1. Respiration chamber (only one is shown).
2. Air conditioners on top and bottom cage tiers.
3. Thermostat.
4. Excreta collection trays.
5. Feeders
6. Cup water drinkers.
7. Separators between feeders.
8. Metal strips to prevent excreta loss.
9. Water-filled channel.
10. Inlet pipe for fresh air.
11. Outlet pipe for chamber air.
12. Inline filter.
13. Flow nozzle.
14. Switching taps.
15. Pressure gauge.
16. Main ventilation diaphragm pumps.
17. Needle valves.
18. Small diaphragm pumps.
19. Solenoid valves.
20. On/Off control tap.
21. Calibration gas cylinders.
22. Dryer (Calcium Chloride).
23. Dryer (Calcium Sulphate).
24. Dryer (Phosphorus pentoxide).
25. Needle valve.
26. On/Off calibration control tap.
27. Three-way tap.
28. Rotameters with needle valves.
29. CO_2 analyser.
30. O_2 analyser.
31. Thermocouple selector unit.
32. Chart recorder.
33. Top view of one respiration chamber.
34. Air conditioner on top cage tier.
35. Air conditioner on bottom cage tier.
36. Thermostat
37. Outlet pipe for chamber air.
38. Inlet pipe for fresh air.

two tiers, upper and lower, each with two wire-mesh layer battery units in a back-to-back arrangement with six single bird cages (457 mm length x 203 mm width) and fitted with individual galvanised iron feeders and small adjustable cup drinkers. Cages can be modified to accommodate the larger broiler breeder birds. Metal strips of galvanised metal with flanges are positioned at the rear and extreme sides of each cage structure to prevent excreta loss. Galvanised sheet metal trays (1120 mm length x 480 mm width x 90 mm height), positioned on angle iron guide-rails, were used for the quantitative collection of excreta. The chamber frames can be elevated and positioned above the cage units to provide access to the birds for the usual routine maintenance tasks.

Two refrigerant air-conditioners (Muller Pty. Ltd., Australia) are positioned above each of the cage tier arrangements, each with a 0.75 kW cooling capacity and thermostatically controlled (Honeywell, USA). Direction of outflow from each air conditioner is reversed in each tier and condensation is directed into the base water-filled channel. These features, in conjunction with air inlet and outlet pipes, are shown in Figure 7.1 . Chamber temperatures are measured with dry and wet bulb thermocouple psychrometers which use copper-constantan wire located at several points around each chamber. The wet bulb thermocouple junctions are surrounded with cotton wick, the end of which is placed in a tube filled with distilled water. Reference "cold" junctions, positioned in a thermos flask filled with ice, are sealed in glass tubes filled with liquid parafin.

7.2.1.3 Mode of operation

Large single-phase electric diaphragm pumps (Thomas Industries, USA), maximal flow 220 dm^3/min, draw air from each of the chambers. Fresh air enters each chamber at a point diagonally opposite to the air outlet via PVC pipes (60 mm diameter) (see Figure 7.1) which draw air from 3.7 m above ground level outside the room. Flow of fresh air into each chamber is regulated to maintain a negative chamber pressure of 4 mm (alcohol gauge) irrespective of the air outflow rate. Effluent chamber air outflow is via PVC pipes (32 mm diameter). Ventilation rate is determined by calibrated brass nozzles (12 mm diameter, 60 mm length) situated anterior to the pumps inlets and which operate on the principles of choked supersonic flow (Shapiro 1953; Emmons 1958). Nozzles with different bore sizes were calibrated *in situ* against a dry gas meter (S.I.M. Brunt) which was previously calibrated against a standard test

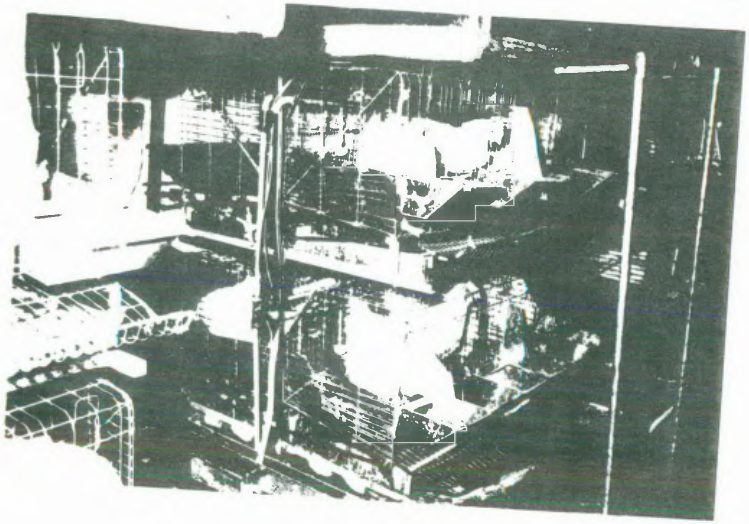
PLATE 7.1: Side view of a respiration chamber showing the metal stands used to raise chamber hoods and the tiered cage arrangement used to house birds. Feeders, excreta collection trays and the watering system are also shown.

PLATE 7.2: Front view of broiler breeders in the cages of the respiration chamber with the plastic covered hood lowered and showing the top cage-tier air conditioner.

PLATE 7.3: Gas analysis and data recording system.

PLATE 7.4: Perspective of measurement systems and respiration chambers. In the background is an extraction fan which was used to maintain air quality during periods when chamber hoods were raised.

Plates



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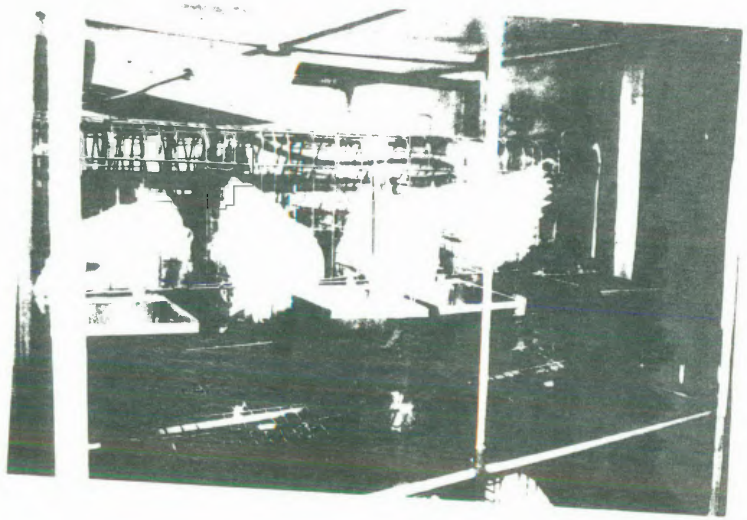

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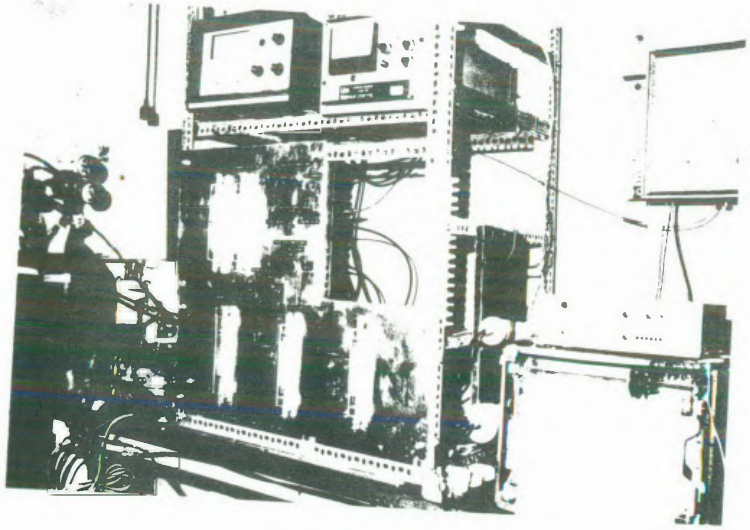

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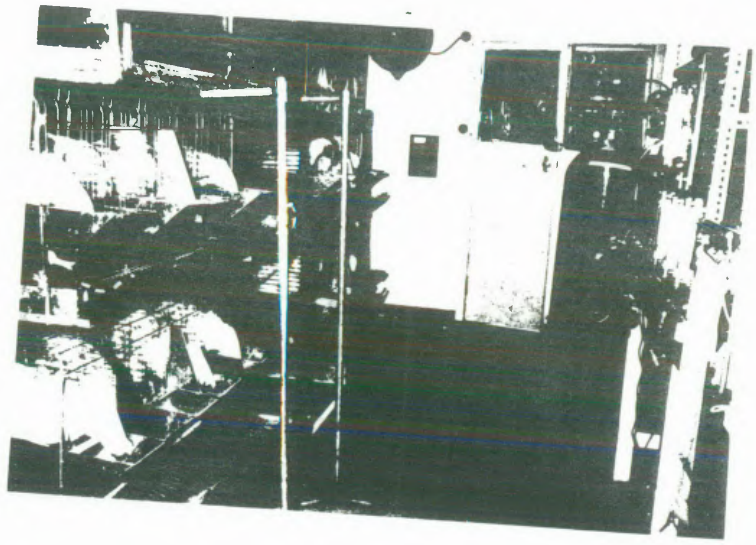

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meter, and which was also compared with a precision wet gas meter (Alexander Wright & Co. Ltd., England) at low flow rates with excellent results. A barometrically independent vacuum gauge (Edwards High Vacuum, England) can continuously monitor pressure in the airline between the nozzle and pump.

Small diaphragm pumps (maximal flow 5 dm^3/min), with adjustable back-flow control valves, sample the effluent chamber gas from the main pump outlets. The sampled gas streams pass through normally closed (denergised) solenoid valves (Goyen Controls, Australia). Fresh air is sampled using a similar arrangement. A modified 12 channel chart recorder (Leeds and Northrup, England) sequentially opens (energises) each of the four solenoid valves which allow samples of gas or fresh air into the gas analysis system.

7.2.1.4 The gas analysis system

From the solenoid valve the gas stream passes through a series of three dryers, the first two of which are constructed of aluminium (60 mm diameter x 250 mm length) and contain calcium chloride ($CaCl_2$, fused lump) and calcium sulphate ($CaSO_4$, "Drierite") respectively. A brass perforated plate placed after the dryer inlets prevents "streaming" and facilitates drying. The third dryer is made of PVC and contains phosphorus pentoxide (P_2O_5) powder, and is designed such that the gas stream passes over rather than through the chemical. Excess flow is removed by opening a needle valve in the gas line between the second and third dryers. The gas stream is subsequently split into two rotameters (Platon, England) by a T-junction. Rotameters are fitted with needle valves which control the gas flow into the carbon dioxide (CO_2) analyser and oxygen (O_2) analyser at 2 dm^3/min and 260 cm^3/min respectively. The infra-red CO_2 analyser (Lira Model 303, Mine Safety Applicances, USA) operates between the range 0-2% CO_2 and is calibrated using dry gases of determined composition: zero gas is nitrogen (N_2), span gas is 1.81% CO_2 in N_2. A paramagnetic oxygen analyser (Model 755, Beckman, USA) which operates on the 20-21% O_2 range, is used to measure O_2 concentration of the sample gas stream. Zero calibration gas is 20.434% O_2 in N_2 (CIG, Australia), while span gas is fresh air of assumed O_2 concentration 20.946% (Machta & Hughes 1970). Calibration gas compositions are measured using a physical absorption technique (Haldane and Priestley 1935).

Nylon tubing (4 mm diameter) is used throughout the gas analysis system. All results are recorded on the Leeds and Northrup, 12 point, 0-1 millivolt recorder, which operates on a print cycle of 3 min/channel at a chart speed of 76.2 mm/hr. Frequent maintenance checks were carried out on all air lines to ensure the absence of leaks prior to calibration tests and calorimetric measurements.

7.2.1.5 Standard calorimetric procedures

With the chamber hoods elevated, the three main ventilation pumps, with air lines disconnected, are started at least 30 min prior to commencement of the period of measurement. The chamber air conditioners are started and checked for proper functioning, and birds are fed in a period of approximately 2 min, usually at 1030 h. Chamber hoods are immediately lowered into the water-filled channels on the chamber base. The chamber air lines are connected to the pump units at 1050 h. This 20 min delay, during which time the gas analysers are calibrated, is designed to avoid the problems encountered with open-circuit calorimeters in the time required to reach steady state (equilibrium) conditions (Depocas and Hart 1957). A similar procedure was adopted by Misson (1974). After a stabilization period of 10 min the small gas sample pumps are started and the period of measurement commenced.

7.2.1.6 Data collection and calculation

A thermocouple selector unit is connected to the recorder such that all thermocouple measurements can be recorded on one recorder channel (channel 7). The print sequence of the variables which is completed in each cycle of the recorder is shown in Table 7.1.

Linear regression equations, derived from calibration and theoretical data, are used to determine dry and wet bulb chamber temperatures, water vapour pressure, relative humidity and barometric pressure. Temperature was calculated from the recorder scale deflection by the equation

$$Y = -0.02301 + 0.27079\ X \qquad (7.1)$$

$$N = 96;\quad R^2 = 0.9997$$

where Y is chamber temperature (^{o}C) and X is the percentage units of recorder deflection. To derive this equation a standard thermocouple was enclosed in a sealed glass capillary tube and immersed in a stirred water bath in close proximity to a precision ($\pm\ 0.1^{o}C$) thermometer (Dobros, Sydney). Temperature of the water bath was varied to achieve a range of recorder outputs. The effective vapour pressure (mm Hg) of the chamber

TABLE 7.1 Print sequence of the various parameters on the chart recorder.

Channel number	Parameter	Chamber number
1	Carbon dioxide	1
2	Oxygen	1
3	Carbon dioxide	2
4	Oxygen	2
5	Carbon dioxide	3
6	Oxygen	3
7	Dry bulb thermocouple	1
	Wet bulb thermocouple	1
	Dry bulb thermocouple	2
	Wet bulb thermocouple	2
	Dry bulb thermocouple	3
	Wet bulb thermocouple	3
8	Oxygen, fresh air	-
9	Carbon dioxide, fresh air	-
10	Oxygen, fresh air	-
11	Carbon dioxide, fresh air	-
12	Oxygen, fresh air	-

air was calculated from the psychromatic equation

$$e = e_w - AP(t-tw)$$

where e_w is the saturation vapour pressure (mm Hg) at the temperature tw, t is the chamber dry bulb temperature (^{o}C), tw is the chamber wet bulb temperature (^{o}C), A is the psychrometric constant and P is the corrected barometric pressure (see Equation 7.3). Theoretical data (Handbook of Chemistry and Physics, 1974) were used to derive an equation over the temperature range 13 to 30^{o}C to estimate the saturation vapour pressure (e_w) at tw

$$\text{Log}_{10}\ (e_w) = 0.71011 + 0.02657 \qquad (7.2)$$
$$N = 31;\quad R^2 = 0.9999$$

The observed barometric pressure, which is read from a barometer with a brass scale, must undergo two corrections, a temperature correction to 0^{o}C and a reduction to gravity at sea level. A multiple linear regression equation was derived from theoretical data (Handbook of Chemistry and Physics, 1974) to determine the temperature correction factor

$$Y = 0.10955X_1 + 0.0036X_2 - 2.46616 \qquad (7.3)$$
$$N = 16;\quad R^2 = 0.9969$$

where Y is the correction to brass scale (mm Hg) which is subtracted from the observed barometer reading, X_1 is the observed barometer temperature (°C), and X_2 is the observed pressure (mm Hg). Reduction to gravity at sea level is equivalent to subtracting 1.07 mm Hg from the observed pressure for Armidale.

Oxygen concentrations in fresh air are used to correct the observed sample gas oxygen concentrations for changes in barometric pressure. Volumetric rates (dm^3/min) of production of CO_2 and O_2 consumption are calculated in the normal way (e.g., MacLean and Watts 1976) over each period of data recording (36 min). When the quotient CO_2/O_2 is less than unity a correction to the observed O_2 consumption is carried out to correct for the systematic error encountered in open-circuit respiration chambers under this condition (Brody 1945; Swift and French 1954; Depocas and Hart 1957; Romijn and Lokhorst 1966; MacLean 1972). The formula given by Misson (1974), with modification, is used for this correction. Gas composition curves are integrated using a computerised algorithmic technique (Gill and Miller 1972) over the total period of measurement (usually 22 h), and, after correction for any change in the volume of carbon dioxide and oxygen in a chamber between the beginning and completion of a measurement period, heat production (HE) is calculated according to the Brouwer (1965) formula without correction for nitrogen (N) metabolism.

$$HE = 16.18\ O_2 + 5.02\ CO_2 \qquad (7.4)$$

where O_2 and CO_2 are in dm^3 of dry gas (STP), and HE is in kJ/24 h.

7.2.2 Calibration and volume estimation of the respiration chambers

Two methods were used to measure equipment function:

(1) infusion of pure carbon dioxide (CO_2) and its recovery; and
(2) combustion of alcohol.

A small CO_2 cylinder (Size D, CIG), fitted with pressure regulators and situated on an electronic pan balance (for initial experiments), passed CO_2 through a sealed water-filled reservoir. The reservoir outlet was connected to a precision wet gas meter which passed the gas into a respiration chamber. A stopwatch was used to record the exact duration of each infusion experiment, which was not commenced until equilibrium had been reached in the chamber CO_2 concentration. The quantities of estimated CO_2 recovered (dm^3, STP) in the effluent chamber gas were compared with the amounts infused (dm^3, STP) through the wet gas meter.

Gas quantities were always corrected for vapour pressure.

Ethyl alcohol ($CH_3CH_2OH_{(l)}$) and propane ($CH_3CH_2CH_{3(g)}$) were combusted in the respiration chambers primarily to check the ratio of carbon dioxide produced to oxygen used (CO_2/O_2) for comparison with theoretical values. The use of propane was discontinued due to incomplete combustion using the available propane burners. For the ethyl alcohol combustion experiments, small flasks filled with ethyl alcohol and which were fitted with rubber stoppers with cotton wicks contained in protruded glass tubes, were placed on an electronic balance inside a chamber. The cotton wicks were ignited and measurement periods started after attainment of equilibrium gas concentrations.

At the completion of some CO_2 infusion studies the infusion was abruptly discontinued and the exponential rate of decline in chamber CO_2 concentration followed in exact time intervals after cessation. These curves were then graphed on a log-linear basis which allowed the volume of each chamber to be calculated by standard isotope dilution theory, according to the formula

$$V = (VR.t_{\frac{1}{2}})/0.693 \qquad (7.5)$$

where V is the estimated chamber volume (dm^3), VR is the ventilation rate (dm^3/min) and $t_{\frac{1}{2}}$ is the half-life of the initial (t = 0) CO_2 concentration in the chamber.

7.2.3 Preliminary biological experiment

7.2.3.1 Management of birds

Ninety seven broiler breeder birds (Hyline), hatched in March 1979, were randomly selected from a trial at the University Poultry Farm in which liveweight during rearing (42-152 d of age) was controlled by limitation of feeding time. Selected birds were placed in flat-deck cages (see Section 2.1.2.2, Chapter 2) situated in a galvanised iron shed without environmental control for 56 d prior to placement in the chambers. During this period lighting was controlled at 17 h light : 7 h dark (17L : 7D), average temperature was 19°C (mean maximum 27°C, mean minimum 11°C), and birds were given controlled quantities daily of a specially formulated commercial laying diet for broiler breeders (diet 3, Chapter 2). Liveweights, feed allowances and production parameters during the 56 d period are given in Table 7.2. At the end of this period, sixty three birds were selected by stratified random sampling (liveweight basis) forty eight of which were placed in the three chambers (16 per chamber), and the remainder maintained as replacements in similar cages in another room.

TABLE 7.2 Feed allowances and production of broiler breeder hens (N = 97) during a two month period prior to placement in respiration chambers.

Age (d)	Liveweight (W, kg)	Feed allowance (g/bird d^{-1})	Egg production	
			per 100 hen d	g/bird d^{-1}
210	2.916(±0.259)+	150	51.7	28.7
217	-	170	59.9	35.1
224	-	170	65.4	39.5
231	-	180	64.9	39.6
238	-	180	65.9	40.6
245	-	180	57.7	35.7
252	-	180	60.9	38.3
259	-	180	58.8	37.3
266	3.539(±0.383)	180	63.3	40.7

+ Standard deviation

7.2.3.2 Experimental feeding regimens

Measurements were not commenced for a further 21 d period after birds were placed in the respiration chambers to allow for acclimation and chamber familiarization; however some preliminary studies were carried out in this period to standardize certain procedures associated with feeding and the logistics of heat production measurement. Lighting was controlled (17L : 7D), room temperature was approximately 20°C and feed allowances were continued at 180 g/bird d^{-1}. Calorimetric measurements commenced when the birds were 294 d of age. Each group of birds in the chambers was allocated to a low, medium and high feeding regimen. Within each of the regimens there were three feeding levels which were randomly allocated to one of the three groups. Quantities of feed allocated were calculated on a liveweight basis for individual birds as a function of their estimated maintenance energy requirement (ME_m, 400 kJ/kgW d^{-1}; Balnave *et al.* 1978; see Table 6.9). The multipliers used to obtain the desired variation in energy balance (RE) and metabolisable energy intake (ME) are given in Table 7.3. Feed residues were weighed daily.

Each period during which the feeding regimens were given was made up of a 4 d adjustment period and a 10 d measurement period which was divided into two 5 d subperiods.

TABLE 7.3 Feeding regimens and the levels of feed allocated to groups as a function of the estimated maintenance energy requirement (ME_m)

Feeding regimen	Multiple of estimated maintenance requirement (ME_m)	Group/Chamber
Low	0.9	1
	1.0	3
	1.2	2
Medium	1.3	2
	1.4	1
	1.5	3
High	1.6	2
	1.7	3
	1.8	1

7.2.3.3 Liveweight

Liveweight was measured, and feed allowances adjusted accordingly, four times during the total 14 d period on a particular feeding regimen: (1) at the beginning of the 4 d adjustment period, (2) at the end of the 4 d adjustment period, (3) at the completion of the first 5 d measurement period and (4) at the end of the second 5 d measurement period. Interpretation of energy metabolism studies which involve large changes in feed intake are often confounded by the influence of gut contents on the measured liveweight since there is insufficient time to allow for minimization of these effects by starvation. Also, in long term energy metabolism studies, the effect of continual intermittent starvation for liveweight measurement *per se* on energetics cannot be discounted. With spare birds available an experiment was carried out to derive a relationship between feed intake and gut contents. Twenty seven birds were offered different quantities of feed between 100g/bird d^{-1} and *ad libitum* (330 g/bird d^{-1}) at 400 d of age for at least 7 d prior to slaughter by cervical dislocation. Birds were weighed and gut contents (crop to rectum inclusive) removed and weighed.

7.2.3.4 Measurement of energy metabolism

The metabolisable energy content of the diet was determined by a bioassay technique (Farrell 1978; Farrell 1980) and found to be 11.58 kJ ME/g (see Section 2.3, Chapter 2). Metabolisability (q,% of GE) of

the diet was 73.9. It was planned to measure heat production (HE) on each day of the 10 d period. The procedures and calculations were given in Section 7.2.1. Mean (±SD) chamber temperatures during measurements of heat production were 21.6 (±0.5) and relative humidity 80-90%. At the completion of the experimental feeding regimens, birds were deprived of feed and heat production (HE) was measured on two groups (1 and 3); a malfunction in a pump unit prevented similar measurements from being carried out on birds in group 2.

7.2.3.5 Egg production

Eggs from individual birds were collected and weighed each day.

7.3 RESULTS

7.3.1 Calibration and volume estimation of respiration chambers

7.3.1.1 Carbon dioxide (CO_2) calibration

Fifty two CO_2 infusion experiments were carried out (N = 20, chamber 1; N = 17, chamber 2; N = 15, chamber 3) with variation in parameters such as ventilation rate, chamber CO_2 concentration and duration of infusion between each experiment. Results are given in Table 7.4. There were no significant differents between chambers in the estimated recovery of CO_2 infused; the mean (±SD) CO_2 recoveries expressed as a percentage of CO_2 infused were 98.4 (±1.7)%, 99.2 (±2.8)% and 98.8 (±2.4)% for chambers 1, 2 and 3 respectively. The relationship between CO_2 recovered (Y, dm^3, STP) and CO_2 infused (X, dm^3, STP) was

$$Y = 1.03\ X - 1.09 \qquad (7.6)$$

$$N = 52;\quad R^2 = 0.998;\quad RSD = 1.31$$

Analysis of this relationship showed no significant differences (P = 0.36) between each of the chambers in the recovery of CO_2 after covariance adjustment for CO_2 infused. Seventeen comparisons were made initially between the CO_2 infused as calculated by both the loss in cylinder weight and simultaneous wet gas meter infusion. The mean (±SD) difference between the wet gas meter infusion and that calculated by loss in cylinder weight was -0.82% (±1.28).

7.3.1.2 Carbon dioxide (CO_2) production and oxygen (O_2) consumption from ethyl alcohol combustion

The mean (±SD) production of CO_2 and consumption of O_2, expressed as a percentage of the theoretical values for all the ethyl alcohol

TABLE 7.4 CO_2 infusion and recovery from respiration chambers

Chamber	Date	Duration of infusion (mins)	Nozzle flow rate (dm^3/min)	(CO_2-0.033)% in effluent	Volume of CO_2 infused (l,STP)	Volume of CO_2 recovered (l,STP)	$(\frac{\text{Recovered}}{\text{Infused}})$%
1	20/ 9/79	41	49.17	0.339	5.60	5.42	96.78
	20/ 9/79	259	49.17	0.348	35.78	35.36	98.83
	3/10/79	159	49.17	0.409	25.15	25.42	101.07
	3/10/79	60	49.17	0.405	9.48	9.51	100.30
	3/10/79	53	49.17	0.403	8.43	8.36	99.15
	24/10/79	67	72.64	0.417	16.98	16.23	95.59
	24/10/79	76	72.64	0.417	19.20	18.39	95.77
	24/10/79	64	72.64	0.415	16.03	15.39	95.99
	25/10/79	68	72.64	0.291	11.74	11.49	97.87
	25/10/79	104	72.64	0.287	17.77	17.29	97.32
	25/10/79	111	72.64	0.285	18.61	18.40	98.84
	25/10/79	80	72.64	1.152	53.49	53.83	100.63
	25/10/79	60	72.64	1.131	39.54	39.67	100.33
	7/12/79	90	87.60	1.134	71.18	70.15	98.56
	7/12/79	69	87.60	1.125	54.21	53.03	97.83
	8/12/79	101	87.60	0.365	26.14	25.42	97.25
	8/12/79	82	87.60	0.365	21.15	20.57	97.28
	4/ 4/80	63	99.02	1.335	67.28	66.50	98.85
	4/ 4/80	89	99.02	1.464	102.53	102.97	100.43
	4/ 4/80	71	99.02	1.535	87.45	86.51	98.92
2	23/ 9/79	193	75.46	0.388	46.68	45.30	97.04
	2/10/69	60	75.46	0.351	13.26	12.96	97.75
	2/10/79	60	75.46	0.359	13.17	13.04	99.04
	2/10/79	62	75.46	0.361	13.70	13.55	98.92
	26/10/79	147	72.64	1.431	122.53	122.26	99.78
	26/10/79	71	72.64	1.416	58.27	58.42	100.25
	27/10/79	87	72.64	0.308	15.84	15.58	98.32
	27/10/79	137	72.64	0.306	24.77	24.26	97.95
	27/10/79	80	72.64	0.303	14.35	14.02	97.69
	9/12/79	75	87.60	0.807	43.01	41.91	97.44
	9/12/79	58	87.60	0.741	30.44	29.65	97.42
	10/12/79	64	87.40	0.402	18.89	18.05	95.56
	10/12/79	76	87.60	0.410	22.34	21.86	97.84
	10/12/79	64	87.60	0.412	18.76	18.46	98.43
	5/ 4/80	91	99.08	1.396	96.80	101.46	104.81
	5/ 4/80	73	99.08	1.355	75.99	80.00	105.29
	5/ 4/80	72	99.08	1.339	75.40	77.93	103.36
3	4/10/80	68	75.46	0.343	14.27	14.00	98.11
	4/10/80	76	75.46	0.337	15.69	15.45	98.49
	4/10/80	66	75.46	0.335	13.68	13.24	96.77
	4/10/80	120	75.46	0.336	24.62	24.12	97.96
	4/10/80	82	75.46	0.337	16.75	16.49	98.44
	16/11/80	80	72.64	1.173	54.19	53.55	98.83
	16/11/80	79	72.64	1.167	53.01	52.64	99.29
	16/11/80	120	72.64	1.158	78.57	79.30	100.93
	16/11/80	247	72.64	1.101	147.86	156.15	105.61
	17/11/80	67	72.64	0.267	10.59	10.45	98.71
	17/11/80	138	72.64	0.263	21.93	21.08	96.11
	17/11/80	75	72.64	0.263	11.76	11.39	96.80
	17/11/80	54	72.64	0.264	8.42	8.21	97.49
	17/11/80	72	97.04	1.153	65.84	64.98	98.70
	6/ 4/80	71	97.04	1.180	64.55	65.55	101.56

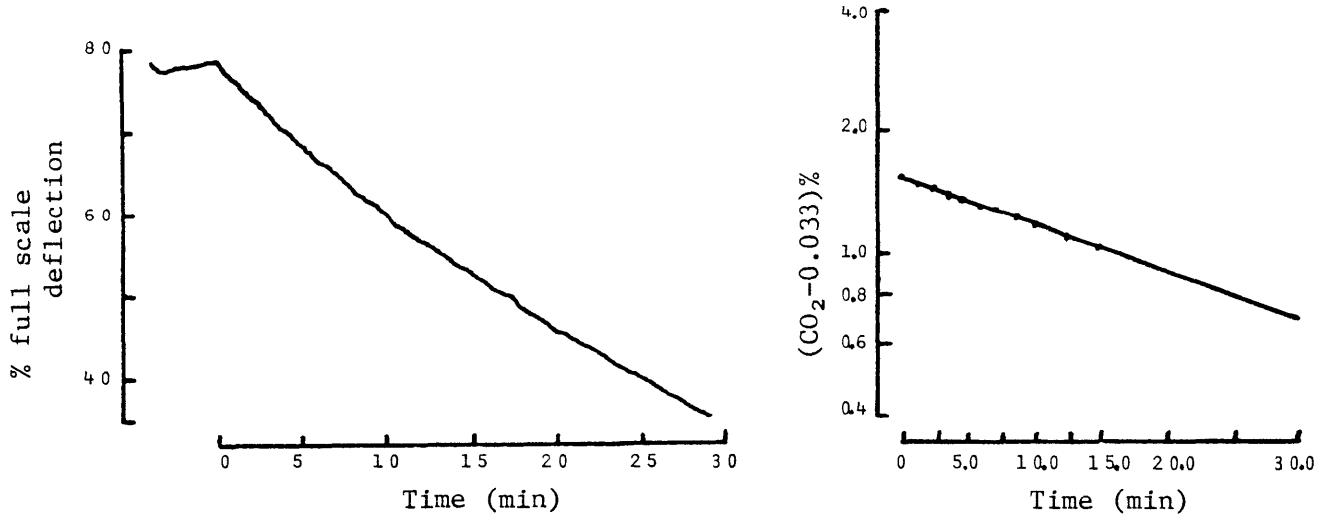


FIGURE 7.2: An actual chart recorder tracing of the pattern of decrease in CO_2 concentration in the effluent air stream from one of the respiration chambers with increasing time after cessation of CO_2 infusion. The log-linear plot of this curve is shown on the right. Curves such as this were used to estimate chamber volume using equation 7.5 given in Section 7.2.2.

combustion experiments (N = 51) were 104.2 (±6.7%) and 103.7 (±6.2%) respectively. The mean (±SD) quotient of CO_2 produced to O_2 consumed (N = 51) was 0.6700 (±0.019). There were no significant differences between the respiration chambers for these variables.

7.3.1.3 Chamber volumes

A typical chart recording from a volume estimation experiment is given in Figure 7.2. The log-linear plot of the data points from the curve shown is also given in Figure 7.2. The mean volumes (±SD) of the chambers were found to be 3406 (±168), 3230 (±240) and 3353 (±185) dm^3 for chambers 1, 2 and 3 respectively.

7.3.2 Preliminary Biological Experiment

Two birds died during the experiment (Bird 5, peritonitis; Bird 8, liver haemorrhage) and were replaced with spare birds of similar liveweights.

7.3.2.1 Liveweight correction for gut contents

Data from two birds were omitted from analysis due to difficulty in the quantitative collection of gut contents. The significant ($P < 0.001$) relationship between weight of gut contents (Y, g) and feed intake in the 24 h prior to slaughter (X, g) was

$$Y = 0.366\ X - 14.3 \qquad (7.7)$$

$$N = 25;\quad R^2 = 0.70;\quad RSD = 22.4$$

This equation was used to obtain corrected liveweights which were subsequently used in all calculations.

7.3.2.2 Feed intake

All birds consumed the allocated feed quantities. Feed intake (g/kgW d^{-1}) for each of the groups of broiler breeders is given in Table 7.4.

TABLE 7.4 Feed intake (g/kgW d^{-1}) of three groups (N = 16 per group) of broiler breeders in respiration chambers. Standard error of the means (SEM) are given in parentheses.

Group	Period 1 a	Period 1 b	Period 2 a	Period 2 b	Period 3 a	Period 3 b
Regimen:	High		Medium		Low	
1	58(±2.8)	54(±1.5)	46(±1.2)	47(±1.1)	32(±0.4)	32(±0.2)
	Low		High		Medium	
2	43(±0.2)	43(±0.1)	54(±0.1)	54(±0.2)	45(±0.3)	45(±0.6)
	Medium		Low		High	
3	51(±1.4)	50(±0.4)	35(±0.3)	36(±0.2)	56(±1.5)	53(±1.1)

7.3.2.3 Liveweight and energy metabolism

Mean liveweight, metabolisable energy intake heat production and respiratory quotient are given in Table 7.5. Heat production was not measured for birds in group 2 during period 3b due to technical difficulties. Retained energy (RE) for this period (3b) was therefore determined using the mean heat production obtained for group 2 in the preceeding period (3a). Only two heat production measurements were carried out in the initial experimental period (1a) due to a malfunction in the recorder (2d downtime) and chamber air conditioners (1d downtime). During one day of each of the periods 1b and 3a there was a problem with the fresh air pump (see Figure 7.1), and another malfunction in the recorder during period 2b; heat production measurements were therefore omitted for one day in periods 1b and 3a and could not be determined for one day in period 2b.

The average coefficients of variation (%, $SD/\bar{X}$) for heat production measured for consecutive days were 2.8, 3.8 and 2.4 for groups (chambers)

1, 2 and 3 respectively. These values would be substantially lower if values obtained at the beginning of the experiment (period 1a), during which most of the technical problems occurred, were omitted. The relationship between retained energy and metabolisable energy intake is shown in Figure 7.3, and the derived linear relationships, both with and without inclusion of starvation heat production (SHP), are given in Table 7.6. Maintenance energy requirement (ME_m), calculated from equations 7.8 and 7.10 was 268.1 kJ/kgW d^{-1} and 366.2 kJ/$kgW^{0.75}$ d^{-1} respectively. Calculated from equation 7.9 and 7.11 these estimates (ME_m) were 308.6 kJ/kgW d^{-1} and 424.5 kJ/$kgW^{0.75}$ d^{-1} repsectively. Efficiency of utiliz-

TABLE 7.5 Mean (±SD) liveweight and mean (±SEM) metabolisable energy intake, respiratory quotient and heat production of three groups of broiler breeder hens (N = 16/group) which received different feed allocations.

Group/ Chamber number	Period	Liveweight+ (W, kg)	Metabolisable energy intake (ME, kJ/bird d^{-1})	Respiratory quotient (RQ)	Heat production (HE, kJ/ bird d^{-1})
1	1a	3.65(0.31)	2435(118)	1.00(0.02)	1438(80)
	1b	3.71(0.31)	2338(65)	0.98(0.05)	1432(61)
	2a	3.78(0.35)	2021(53)	0.98(0.03)	1368(20)
	2b	3.82(0.38)	2057(49)	1.00(0.04)	1371(43)
	3a	3.68(0.37)	1348(16)	0.83(0.06)	1122(17)
	3b	3.60(0.36)	1330(9)	0.92(0.02)	1073(22)
2	1a	3.49(0.27)	1728(8)	0.96(0.06)	1098(96)
	1b	3.46(0.30)	1711(3)	0.96(0.02)	1114(35)
	2a	3.63(0.33)	2266(5)	1.04(0.04)	1354(19)
	2b	3.70(0.35)	2299(9)	1.04(0.01)	1356(9)
	3a	3.71(0.36)	1913(14)	0.98(0.02)	1173(57)
	3b	3.69(0.38)	1906(24)	-*	-*
3	1a	3.62(0.40)	2126(59)	0.98(0.02)	1348(86)
	1b	3.66(0.41)	2109(17)	0.96(0.04)	1370(37)
	2a	3.59(0.43)	1467(12)	0.98(0.04)	1177(18)
	2b	3.54(0.43)	1461(8)	1.02(0.03)	1117(15)
	3a	3.76(0.46)	2437(65)	1.04(0.01)	1422(18)
	3b	3.85(0.48)	2360(48)	1.05(0.01)	1430(12)

* Not measured due to equipment failure.

\+ Liveweight corrected for gut contents for individual birds.

TABLE 7.6 Values of the coefficients (±SE) in the relationship between retained energy and metabolisable energy intake (RE = a+bME) both with and without inclusion of starvation heat production.

Dependent (RE) and independent (ME) variables	Inclusion(+) or exclusion (-) of SHP	Coefficient (±SE) a	Coefficient (±SE) b	N	R^2	RSD	Equation number
kJ/kgW d^{-1}	-	-186.3(±23.4)	0.695(±0.042)	18	0.938	17.1	7.8
kJ/kgW d^{-1}	+	-250.6(±12.8)	0.812(±0.025)	20	0.983	20.3	7.9
kJ/kgW$^{0.75}$ d^{-1}	-	-251.6(±32.8)	0.687(±0.044)	18	0.935	24.3	7.10
kJ/kgW$^{0.75}$ d^{-1}	+	-341.3(±18.1)	0.804(±0.025)	20	0.981	28.9	7.11

† N is number of observations, R^2 is the correlation coefficient and RSD is the residual standard deviation.

ation of metabolisable energy for production (kp) was approximately 70%, and efficiency of utilization of metabolisable energy for both maintenance and production (km + p), assuming complete linearity of the relationship between retained energy and metabolisable energy intake, was 80%.

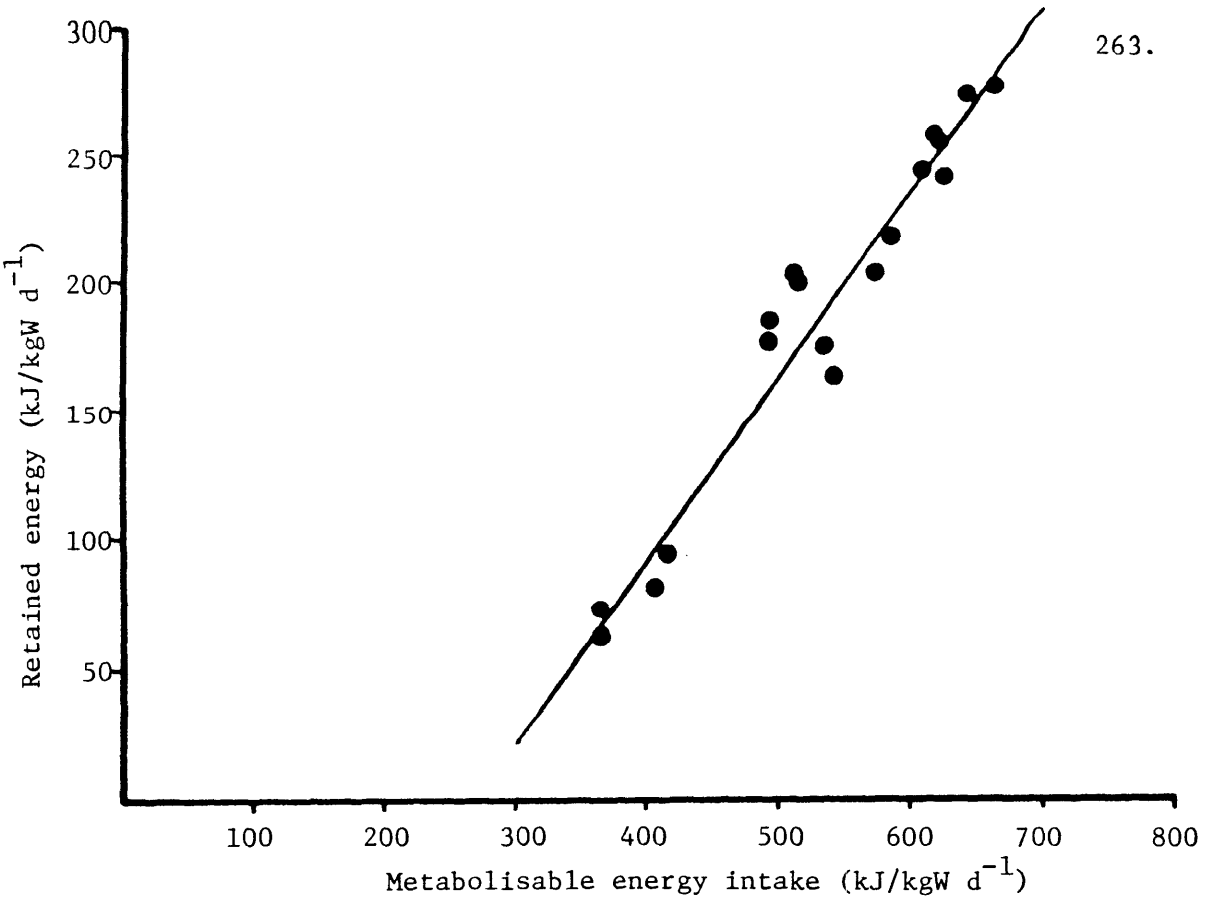
Starvation heat production determined on two groups of broiler breeders (1 and 3) at the completion of the experimental feeding regimens are given in Table 7.7.

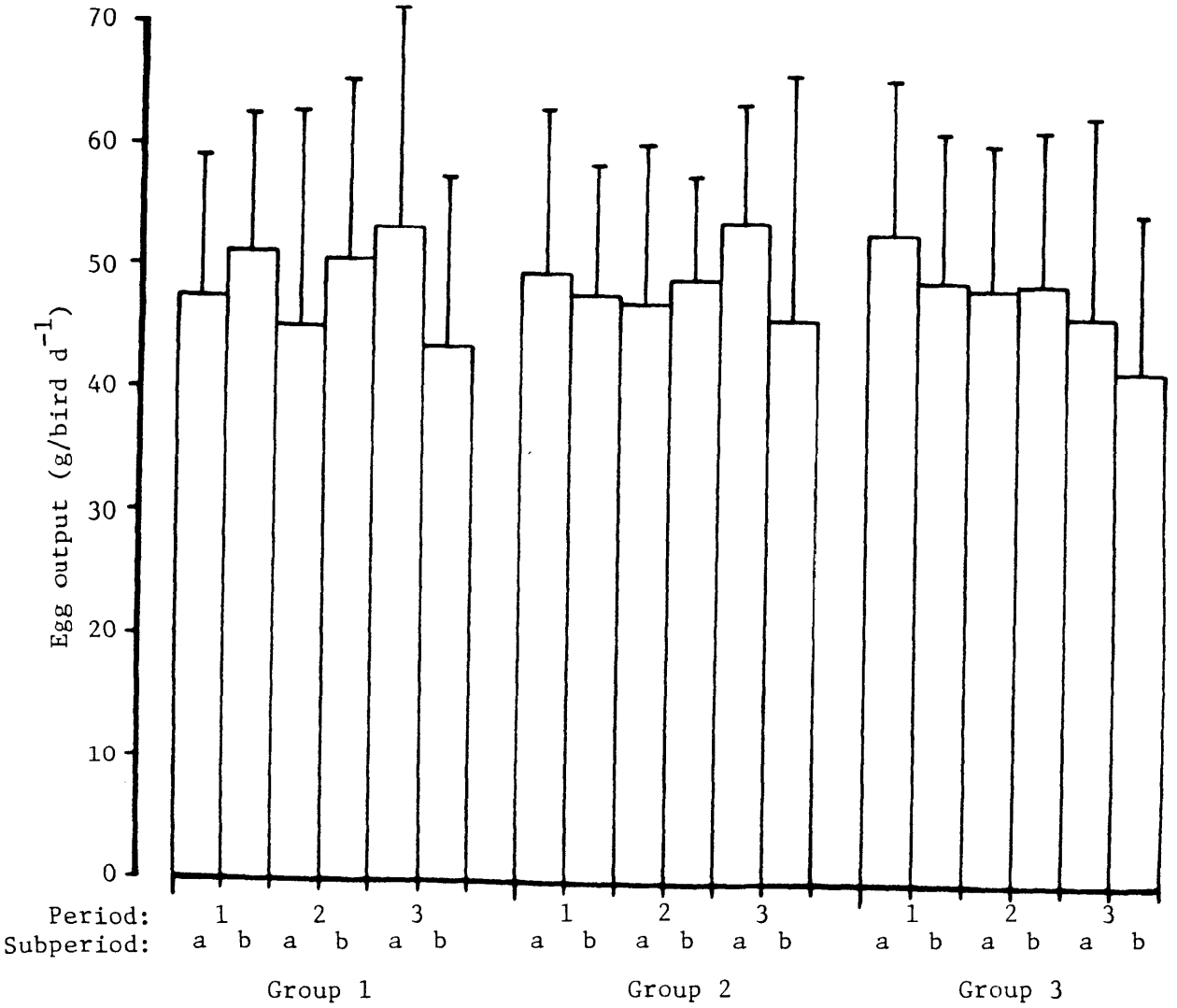
TABLE 7.7 Starvation heat production and respiratory quotient in two groups (N = 16) of broiler breeders

Group	Starvation time (h)	Respiratory quotient (RQ)	Liveweight (W, kg)	Starvation Heat Production (SHP) kJ/bird d^{-1}	kJ/kgW d^{-1}	kJ/kgW$^{0.75}$ d^{-1}
1	24-48	0.700	3.47	887.6	256.1	349.4
	48-72	0.677	3.37	860.0	255.4	346.0
3	24-48	0.723	3.72	965.7	259.8	360.8
	48-72	0.711	3.61	917.4	254.2	350.3

FIGURE 7.3: The relationship between retained energy (RE, kJ/kgW d^{-1}) and metabolisable energy intake (ME, kJ/kgW d^{-1}) for three groups of broiler breeder birds (N = 16/group) each of which received three feeding levels for two 5 d periods per level. The fitted line is the regression equation: RE = -186.3 + 0.695 ME.

FIGURE 7.4: Mean egg output (g/bird d^{-1}) of groups of broiler breeders which received varied feed allocations in respiration chambers. Vertical bars are the positive standard deviations (SD) of means.


Retained energy (kJ/kgW d^{-1})
300
250
200
150
100
50
100
200
300
400
500
600
700
800
Metabolisable energy intake (kJ/kgW d^{-1})


Egg output (g/bird d^{-1})
70
60
50
40
30
20
10
0
Period: 1 2 3 1 2 3 1 2 3
Subperiod: a b a b a b a b a b a b a b a b a b
Group 1
Group 2
Group 3

7.3.2.4 Egg production

Mean (±SEM) egg production (number/100 hen d) was 73.4 (±5.0) for all groups over all measurement periods. This compares extremely well with egg production prior to placement in the respiration chambers (see Table 7.2). Egg output (g/bird d^{-1}) for individual experimental periods is given in Figure 7.4.

7.4 DISCUSSION

7.4.1 Respiration chambers

The respiration chambers described here have the advantage over the smaller units commonly used for studies on poultry (Farrell 1972; Misson 1974; Lundy *et al.* 1978) of allowing long term trials to be carried out on groups of poultry under conditions which better reflect those in practice. Problems such as adaptation to chamber surroundings and behavioural modifications are minimised. Misson (1974) found that oxygen consumption of laying hens decreased by 20% during a 3 d training period in single respiration chambers, a finding which was attributed to adjustment to the experimental conditions. There are reports on calorimetric observations of poultry in which the *ad libitum* feed intake of birds was lower than that predicted or expected (Farrell 1975; Balnave *et al.* 1978; MacLeod and Shannon 1978). Reports on the effects of confinement in respiration chambers on other animal species appear to conflict (Webster *et al.* 1972; Blaxter 1974; Graham and Searle 1975; Thomson 1979; Gray and McCracken 1980), but Blaxter (1974) showed that, at least in sheep, the gaseous and noise environment of the chamber and equipment did not contribute to the observed initial high metabolic rates measured on constant feed regimens. The main factor was the extent of prior confinement. Thomson (1979) reported substantial feed refusal by lambs during calorimetric measurements, but this did not occur with cattle. Similarly, Graham and Searle (1975) found that sheep in respiration chambers had a lower feed intake than penned sheep. Gray and McCracken (1980) showed no effect on heat production of chamber confinement *per se* in pigs conditioned to metabolism cages for at least 10 d prior to measurement. This confirmed the work of Blaxter (1974) and illustrates a major difference between this work (Blaxter 1974; Gray and McCracken 1980) and usual studies with poultry. For example poultry are commonly housed in multiple bird units; they are than removed and placed in single chambers containing cages that are unlike the holding cages. This means that poultry normally have

no direct familiarisation with the measurement cage units, unlike the sheep of Blaxter (1974) and the pigs of Gray and McCracken (1980), and partly explains the effects found in poultry by Misson (1974).

Other factors which could account for some of the effects of confinement on heat production of laying hens observed by Misson (1974) and on feed intake by MacLeod and Shannon (1978), are aberrations in social facilitation traits. The influence of social structure on production parameters in caged egg producing birds was shown by James and Foenander (1961), and more recent studies clearly showed that behaviour may affect feeding patterns and that modifications to group structure may accordingly influence feed intake (Hughes 1971; Davis and Sykes 1977). Changes in important production parameters such as feed intake due to social facilitation, with a consequent shift in the measurement range of the relationship between retained energy and metabolisable energy intake, may therefore occur in situations common to normal calorimetric measurements. Changes in certain other behavioural patterns, such as the amount of time which birds stand (van Kampen 1976c), and the duration of increased activity prior to oviposition (van Kampen 1976a), may also be effected by confinement during calorimetric measurements. These factors may partially explain the range of values reported for the maintenance energy requirement and energetic efficiency in addition to those factors discussed in Chapter 6 (Section 6.4.2). The respiration chambers described in this chapter allowed the birds to be continually housed both prior to and for the duration of the experimental period. Although the applicability of results to the practical situation is undoubtedly enhanced by this procedure, the accuracy of determination of the more theoretical aspects of energy metabolism may also be improved. However, by necessity for calorimetric measurements, broiler breeders must be housed in cages rather than on deep-litter. This difference should be recognized in the studies reported on broiler breeders in this thesis.

Other workers have reported respiration chambers suitable for poultry and constructed of a basic framework covered with a transparent plastic and designed to house groups of birds (Grimbergen 1970; van Es *et al.* 1970). However, these were single chambers which could house only a few laying hens. Continued accurate measurement of the ventilation rates required for large open-circuit respirometers is difficult (Blaxter *et al.* 1972), and often requires constant recalibration of the flow analysis system used. This problem is compounded by lack of availability of

accurate test meters and experiments of long duration. Ventilation rate control for the respiration chambers described in the present study is by specially calibrated flow nozzles, the use of which was originally advocated in open-circuit systems by Chasteau and Cronje (1974). Pressure reduction in the air line between the nozzle and the pump, equal to approximately half of the prevailing barometric pressure, results in static airflow through the nozzle. This condition can be continually monitored in the present system by a barometrically compensated vacuum gauge.

Quantitative infusion of pure gas or gas mixtures (CO_2/N_2) and recovery studies in conjunction with alcohol combustion tests provide a reliable estimation of the precision of the equipment. Such calibration procedures have been used successfully by other workers to provide this information (e.g. Hammel and Hardy 1963; Thorbeck 1969; Verstegen *et al.* 1971; Gray and McCracken 1980), although recently more sophisticated methods have been employed (Lundy *et al.* 1978). The carbon dioxide recovery experiments described gave acceptable results for all flow rates, chamber gas concentrations and infusion times studied. There was an apparent overestimation of carbon dioxide produced and of oxygen consumed calculated from the theoretical production and consumption of these gases with combustion of measured quantities of ethyl alcohol in the respiration chambers, but the quotient (CO_2/O_2) was satisfactory. Puller *et al.* (1969) found considerable variation in the quantities of carbon dioxide produced and of oxygen consumed by combustion of ethyl and methyl alcohol. These results were attributed to incomplete combustion of the alcohol. However, Blaxter *et al.* (1972), Hammel and Hardy (1963) and Misson (1974), obtained good estimates of the theoretical quotient, findings which would be unexpected if alcohol combustion were incomplete or variable.

7.4.2 Preliminary biological experiment

The variation in consecutive heat production measurements within groups of birds on controlled feed intakes was acceptable (Blaxter *et al.* 1972; De Kay *et al.* 1976; Gray and McCracken 1980) and would be expected to be lower in subsequent experiments due to technical refinements and increased standardisation of procedure. Problems were initially encountered in most facets of the calorimeter system, but there were repeated problems with the recorder. However, on the basis that the experiment reported was preliminary in nature the feeding regimens were continued despite lack of the planned number of heat production measurements. Nevertheless, there were at least two heat production measurements in any one experimental subperiod (5 d), and it was considered acceptable for these to be extrapol-

ated to the total subperiod for calculation of the amount of retained energy (e.g. Burlaeu *et al.* 1974; Chwalibog *et al.* 1978).

Heat production and the respiratory quotients found after appropriate feed deprivation were within the range of those reported in other studies on poultry (see Table 6.4, Chapter 6). The only comparable estimate of starvation heat production for birds of similar liveweight is from the study of Balnave *et al.* (1978) who found a mean value of 297 kJ/kgW d^{-1} or 394 kJ/kg$W^{0.75}$ d^{-1} for broiler breeders (W = 3.11 kg). For birds in group 1 there was no further decline in starvation heat production between 48 and 72 h after starvation, but there was a 2% decline in this period for birds in group 3. This was probably due to prior feeding levels; birds in group 1 were on a low feed intake prior to commencement of starvation, whereas birds in group 3 were on a high feed intake prior to commencement of starvation (see Table 7.4). This shows the importance of level of feed intake prior to determination of starvation heat production in conjunction with liveweight (Misson 1974) as determinants of attainment of the post-absorptive state in poultry. Similar results were reported for other animal species (e.g. Marston 1948).

The influence of inclusion of starvation heat production on the linear relationship between retained energy and metabolisable energy intake was clearly demonstrated in this preliminary study (see Table 7.6). There was a marked effect on both the estimated maintenance energy requirement and energetic efficiency due to the inclusion of starvation heat production; recalculation of the results from other studies also showed this effect, particularly on the efficiency of utilization of metabolisable energy (see Table 6.9, Chapter 6), and indicates that the normal assumption (Farrell 1975; MacLeod and Shannon 1978) of complete linearity between retained energy and metabolisable energy intake for maintenance and production is not valid. The maintenance energy requirements estimated without inclusion of starvation heat production were considerably below those obtained by Balnave *et al.* (1978) for broiler breeders, but similar to another study (Grossu *et al.* 1976) which used a heavy breed of bird (Rock). However the efficiency of utilization of metabolisable energy for production was similar for both the present study of the one of Balnave *et al.* (1978). Some of the possible reasons for the difference in the maintenance energy requirement found between the two studies were considered previously (see Chapter 6). However, there is the distinct possibility that the differences may reflect real variation in energy

metabolism due to genetic differences of the strains involved: Balnave *et al.* (1978) used a strain from Allied Genetic Breeders (Pty. Ltd.) whereas the present study used Hyline broiler breeders. Tasaki and Sakurai (1969) found that cross-bred cockerels could be divided into two groups on the basis of basal metabolic rate (280 $kJ/kgW^{0.75}$ d^{-1} and 260 $kJ/kgW^{0.75}$ d^{-1}); Pym and Farrell (1977) found large differences in starvation heat production and maintenance energy requirements in growing broiler birds due to different selection criteria; Farrell (1975) found differences in starvation heat production and maintenance energy requirement between White Leghorns, Australorps and their cross.

Summary

The design and function of three large open-circuit respiration chambers for groups of poultry were described. Three main reasons were given for the approach adopted: (1) the desire to study energy metabolism of birds without modification of dietary treatments for calorimetric measurements *per se*, (2) to orientate the results obtained on energy metabolism to those on production, (3) to minimize the influence on energy metabolism of chamber confinement *per se*, and (4) to optimize equipment usage. Basically the chambers consist of a tiered cage arrangement which is hermetically sealed with a plastic covered hood during periods of measurement of gaseous exchange (CO_2 and O_2). Ventilation rate is controlled by calibrated choked-flow nozzles. Methods used for data recording and calculation were described. Calibration tests with pure CO_2 infusion and ethyl alcohol combustion showed that the performance of the system was acceptable.

The mean CO_2 recovery as a percentage of infused was 98.4, 99.2 and 98.8 for chambers 1, 2 and 3 respectively, and the mean quotient of CO_2 produced to O_2 consumed with combustion of ethyl alcohol was 0.6700. A preliminary study on the energy metabolism of broiler breeders (N = 16/chamber) was carried out to eliminate managerial, procedural and technical problems and to give initial information on energetics of broiler breeders. The average coefficients of variation in consecutive heat production measurements were 2.8, 3.8 and 2.4 for chambers 1, 2 and 3 respectively. The efficiency of utilization of metabolisable energy for production was 70%, and the estimated maintenance requirement was 366 $kJ/kgW^{0.75}$ d^{-1}. Mean starvation heat production was 352 $kJ/kgW^{0.75}$ d^{-1}.